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Gopher Tortoise (*Gopherus polyphemus*) Densities in Coastal Scrub and Slash Pine Flatwoods in Florida

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Abstract.—**Densities of gopher tortoises were compared with habitat characteristics in scrub and in flatwood habitats on the Kennedy Space Center, Florida. Tortoises were distributed widely among habitat types and did not have higher densities in well-drained (oak-palmetto) than in poorly-drained (saw palmetto) habitats. Fall densities of tortoises ranged from a mean of 2.7 individuals/ha in disturbed habitat to 0.0 individuals/ha in saw palmetto habitat. Spring densities of tortoises ranged from a mean of 2.5 individuals/ha in saw palmetto habitat to 0.7 individuals/ha in oak-palmetto habitat. Densities of tortoises were correlated positively with the percent herbaceous cover, an indicator of food resources. Plots were divided into three burn classes; these were areas burned within three years, burned four to seven years, and unburned for more than seven years prior to the study. Relationships between densities of tortoises and time-since-fire classes were inconsistent.**

Most studies of the gopher tortoise (*Gopherus polyphemus*) have been in well-drained longleaf pine (*Pinus palustris*)-turkey oak (*Quercus laevis*) communities known as sandhill, or in pine plantations that were once sandhill. Habitat requirements of tortoises are well-drained, loose soil (Landers and Speake, 1980; McRae et al., 1981; Auffenberg and Franz, 1982; Diemer, 1986). Most tortoises on the Kennedy Space Center, Florida (KSC), occupy scrub and pine flatwood habitats (Breininger et al., 1991a). Little is published on tortoise densities in these habitats. Our objectives were to compare densities of tortoises in scrub and pine flatwood habitats and to investigate the influence of time since the last fire on densities of tortoises.

Materials and Methods

The KSC is the largest protected barrier island complex on the east coast of Florida. It has both temperate and subtropical plant and animal associations. Topographic relief on KSC ranges from sea level to 3 m. Scrub and pine flatwoods (Abrahamson and Hartnett, 1990; Myers, 1990; Schmalzer and Hinkle, 1992b) are the major upland habitat types and are interspersed among seasonally and permanently flooded swale marshes. The understory of pine flatwoods on KSC essentially is identical to scrub; pine flatwoods have a sparse canopy of slash pines (*P. elliotii*). We do not distinguish scrub and pine flatwoods hereafter. Scrub on KSC has a dense shrub layer dominated by myrtle oak (*Quercus myrtifolia*) and sand live oak (*Q. geminata*) on drier sites, and by saw palmetto (*Seronoa repens*) on wetter sites (Schmalzer and Hinkle, 1992a, b). Nearly half the scrub is predominated by saw palmetto, and the remainder is predominated by a mixture of scrub oaks and saw palmetto (Breininger et al., 1991b). Oak-palmetto habitat on KSC often is referred to as oak scrub (Myers 1990) or scrubby flatwoods (Abrahamson and Hartnett, 1990). Saw palmetto habitat is sometimes referred to as mesic flatwoods (Abrahamson and Hartnett, 1990). Fire has little influence on species composition because oaks, palmettos, and ericaceous shrubs resprout from rhizomes (Schmalzer and Hinkle, 1992a, b). The dominant herbaceous plant is wiregrass (*Aristida stricta*). Sites that were historically scrub and were cleared ≥20 yr before the study were termed "disturbed habitat." These were revegetated by scrub species but remain different from scrub in both the relative abundance of scrub plants and structure (Breininger and Schmalzer, 1990).

We established 112 30 × 50 m plots in a stratified random design throughout scrub and flatwoods on KSC (Breininger et al. 1991a). This plot size was the largest size that allowed sampling within homogeneous vegetation. Sixteen plots were established in disturbed habitat, and thirty-two plots were established in each of three burn classes of oak-palmetto and saw palmetto habitat. Burn classes included areas burned within three years, burned four to seven years, and unburned for more than seven years prior to the study. We identified all tortoise burrows within each plot in early fall (September–October 1985) and spring (April–May, 1986). Burrows were classified as active, inactive, or abandoned. Active burrows had recent plastral slide

TABLE 1. Mean (+1 SD) of broad habitat features distinguishing oak-palmetto, saw palmetto, and disturbed habitats on John F. Kennedy Space Center, Florida.

	Habitat types		
	Disturbed (N = 15)	Oak-palmetto (N = 48)	Palmetto (N = 40)
Total shrub cover (%)	63 (29)	98 (3)	96 (8)
Scrub oak cover (%)	28 (29)	57 (24)	14 (9)
Saw palmetto cover (%)	7 (14)	44 (23)	55 (23)
Depth to water table (cm)	84 (39)	84 (38)	55 (24)

marks and footprints (Auffenberg and Franz, 1982). Inactive burrows were recently maintained but lacked fresh sign of use. Abandoned burrows were filled partly with litter or partially caved in. We used a stick method and bucket traps in fall, and a camera system in spring, to determine if adult and subadult burrows were occupied by tortoises (Breininger et al., 1991a). Occupancy of only active burrows was determined in fall; occupancy of both active and inactive burrows was determined in spring. Only one of 44 inactive burrows was occupied by a tortoise; thus, inactive burrows contributed little to densities of tortoises within plots in spring (Breininger et al., 1991a). Burrows ≥12 cm wide at the entrance were classified as subadult or adult burrows; burrows <12 cm wide at the entrance were classified as hatchling or juvenile burrows (Diemer, 1992a). Active juvenile and hatchling burrows were recorded for each plot only during the spring of 1986.

Vegetation measurements were taken at each plot during summer (June–September 1985) using a point-intercept sampling technique (Mueller-Dombois and Ellenberg, 1974). Plots were sampled using a grid of 20 points spaced 5 m apart on four parallel lines across the plot. Lines were spaced 10 m apart. Species of trees, shrubs, herbs, and shrub height were recorded at each point. Slash pine was the only canopy tree present; all other woody plants were shrubs. Water table measurements were taken by coring in fall (September–October 1985) at all plots. Among oak-palmetto and saw palmetto plots, we noted small (<2 m wide) mechanical disturbances (clearing), which we referred to as mild disturbance.

Of the original 112 plots, eight plots were burned during the study and one was cleared; these were excluded from analyses. Densities of tortoises were calculated for each plot, separately for each season, by summing the number of tortoises occupying the burrows in a plot and dividing by the area of the plot.

The percent shrub cover, scrub oak cover, saw palmetto cover, herbaceous cover, and non-*Aristida* herbaceous cover were variables determined for each plot by summing the number of points where the variable was present, dividing by the total of 20 grid points, and multiplying by 100. The calculation of each was independent of others. Non-*Aristida* cover includes ground cover by herbs other than wiregrass. A herbaceous cover variable that excluded wiregrass was selected because other herbs may be better predictors of quality food sources (Garner and Landers, 1981; Macdonald and Mushinsky, 1988). The mean shrub height was determined for each plot by summing the height measurements for each point and dividing by 20.

Scrub plots, which did not include plots in disturbed habitat, were classified as an oak-palmetto habitat if they had ≥30% oak cover or as a saw palmetto habitat if they had <30% oak cover based on field data. Therefore, we analyzed a total of three habitat types: oak-palmetto, saw palmetto, and disturbed. Mean values of habitat features (total shrub cover, scrub oak cover, saw palmetto cover, and distance to water table) were calculated for the three habitat types because these change little with fire history in the burn classes considered here (Schmalzer and Hinkle, 1992a, b). Mean values for habitat variables influenced by fire history (mean shrub height, herbaceous cover, non-*Aristida* herbaceous cover) were calculated for disturbed habitat and for each fire class within oak-palmetto and saw palmetto habitats. Densities of tortoises also were calculated for disturbed habitats and for each fire class within oak-palmetto and saw palmetto habitats. Tortoise densities were not normally distributed in either season (Kolmogorov-Smirnov test [fall]: $z = 5.07$, $P < 0.001$, $N = 103$; [spring] $z = 4.86$, $P < 0.001$, $N = 103$) (SPSS Inc., 1988), preventing the use of parametric statistics.

We calculated Spearman rank correlations among fall and spring tortoise densities and habitat variables by season using data from all plots. The presence or absence of mild distur-

TABLE 2. Mean (+1 SD) of habitat characteristics and of gopher tortoise densities (individuals/ha) for disturbed habitat and time-since-fire classes (0–3, 4–7, >7 years) within oak-palmetto and saw palmetto habitats.

	Disturbed	Oak-Palmetto			Saw Palmetto		
	(N = 15)	0–3 (N = 10)	4–7 (N = 18)	>7 (N = 20)	0–3 (N = 19)	4–7 (N = 9)	>7 (N = 12)
Habitat characteristics							
Mean shrub height (cm)	130 (76)	80 (22)	92 (15)	156 (66)	79 (24)	106 (11)	137 (27)
Herbaceous cover (%)	76 (23)	62 (27)	38 (29)	24 (23)	66 (19)	64 (18)	45 (30)
Non-Aristida herbaceous cover (%)	71 (26)	34 (30)	9 (19)	4 (6)	30 (22)	19 (18)	28 (26)
Gopher tortoise density							
Fall	2.7 (4.9)	1.3 (2.8)	0.4 (1.6)	0.3 (1.5)	2.1 (3.9)	0.0 (0)	2.2 (4.3)
Spring	2.2 (4.8)	0.7 (2.1)	1.1 (2.5)	1.3 (2.8)	2.5 (4.0)	1.5 (3.0)	1.1 (2.6)

bance was treated as a categorical variable to investigate its influence on density of tortoises in oak-palmetto and saw palmetto habitats.

RESULTS

Disturbed habitat did not have as extensive shrub cover as oak-palmetto and saw palmetto habitat (Table 1). Mean depth to the water table was <1 m below the surface in all habitat types. Disturbed habitat had the most herbaceous cover (Table 2). Most of the herbaceous cover was wiregrass in oak-palmetto and saw palmetto habitat. Herbaceous cover in disturbed habitat was diverse and included only small amounts of wiregrass. Recently burned oak-palmetto plots had much higher herbaceous cover than unburned oak-palmetto plots (Table 2).

Many plots in each habitat type had no tortoises, although all but one plot had at least one active or inactive burrow. The plot with no active burrows had active burrows nearby. Standard deviations of densities of tortoises were higher than the means for each habitat type during each season (Table 2). Mean adult and subadult densities of tortoises were usually higher in disturbed habitat than in most oak-palmetto and saw palmetto habitat. Densities of tortoises in saw palmetto habitat exceeded those in oak-palmetto habitat in most seasons and time-since-fire categories, or the differences were small (Table 2). No consistent trends in densities of tortoises occurred among time-since-fire classes in oak-palmetto or saw palmetto habitat.

Only four habitat variables had significant correlations with either fall or spring densities of tortoises and the correlation coefficients were small (Table 3). Only non-*Aristida* cover had significant correlations in both seasons. Time since fire was correlated with herbaceous cover ($r = -0.40$, $P < 0.01$, $N = 103$) and non-*Aristida* herbaceous cover ($r = -0.25$, $P = 0.01$, $N = 103$). Herbaceous cover was highest in plots burned within three years of the study. Herbaceous cover declined more with increasing time-since-fire classes in oak-palmetto habitats than in saw palmetto habitats.

Average densities of hatchling and juvenile burrows were 0.9 (SD = 1.6) burrows/ha for disturbed habitat, 0.7 (SD = 1.3) burrows/ha for oak-palmetto habitat, and 2.3 (SD = 3.6) burrows/ha for saw palmetto habitat. Average densities of hatchling and juvenile burrows were 0.9 (SD = 1.6) burrows/ha in recently burned habitat, 1.0 (SD = 1.7) burrows/ha in habitat burned 4–7 years ago, and 2.5 (SD = 3.7) burrows/ha in habitat unburned for >7 years.

TABLE 3. Spearman rank order correlations (r) between habitat variables and fall and spring gopher tortoise densities on John F. Kennedy Space Center, Florida.

Habitat Parameter	Fall N = 103 r	Spring N = 103 r
% scrub oak cover	−0.21 ($P \leq 0.05$)	−0.11 ($P > 0.05$)
% herbaceous cover	0.06 ($P > 0.05$)	0.23 ($P \leq 0.01$)
% non-*Aristida* herbaceous cover	0.20 ($P \leq 0.05$)	0.23 ($P \leq 0.01$)
Mild disturbance	0.02 ($P > 0.05$)	0.22 ($P \leq 0.05$)

DISCUSSION

Active gopher tortoise burrows occurred within or adjacent to all study plots suggesting that tortoises were widely distributed in these habitats. Only 20-29% of these burrows were occupied (Breininger et al., 1991a), probably because tortoises used several burrows and frequently relocated to new burrows (e.g., McRae et al., 1981; Douglass, 1990; Diemer, 1992b). Seasonal habitat shifts may have occurred but cannot be determined given the high variation in densities of tortoises. Herbaceous cover had greater influence on density of tortoises elsewhere (Auffenberg and Iverson, 1979; Garner and Landers, 1981) than we observed among our plots. Herbaceous cover within plots may be a poor indicator of available food resources, because swale marshes were near plots, and tortoises fed in them (Breininger et al., 1988).

Densities of tortoises were higher in disturbed habitats than in oak-palmetto and saw palmetto habitats, as expected (Auffenberg and Franz, 1982). Disturbed habitats have fewer shrubs and a more abundant and diverse herbaceous layer than oak-palmetto and saw palmetto habitats (Breininger and Schmalzer, 1990) which may explain the higher densities of tortoises in disturbed habitat. Tortoises will move long distances to find nesting sites, and they select sunny openings (Hallinan, 1923; Landers and Speake, 1980; Landers et al., 1980). The positive correlation between density of tortoises in spring and mild disturbance in oak-palmetto and saw palmetto habitats may be related to nest site selection or basking needs. Open areas, common in disturbed habitats, are rare in most oak-palmetto and saw palmetto habitats except for small areas showing mild soil disturbance associated with historical logging or turpentining activities (Schmalzer and Hinkle, 1992a, b). Disturbed habitat, which had major soil disturbance, is occupied by tortoises for at least 20 yr after clearing; the regenerated habitat often burns poorly and can become less suitable for tortoises and other species of conservation concern (Breininger and Schmalzer, 1990).

The need for periodic fire to maintain suitable tortoise habitat is well established (Landers, 1980; Landers and Speake, 1980; Auffenberg and Franz, 1982; Diemer, 1986). Densities of tortoises, however, were not always higher in the most recently burned plots, and tortoises occurred in areas unburned for more than 20 years. Food resources were more abundant in recently burned oak-palmetto and saw palmetto plots than in unburned plots, but even unburned plots were near swale marshes where food was abundant.

Densities of tortoises were not usually higher in oak-palmetto (well-drained) than in saw palmetto (poorly-drained) plots in spring or fall. We reported that tortoises did not select well-drained sites in winter (Breininger et al., 1991a). Most studies suggest that well-drained conditions are required by gopher tortoises (e.g., Landers and Speake, 1980; Auffenberg and Franz, 1982), although some note exceptions (Means, 1982; Diemer, 1986). Also, tortoises had slightly higher densities in saw palmetto than in oak-palmetto in another study on KSC, perhaps because more food is near burrows in saw palmetto habitat (Giovanetto, 1988).

Most studies of habitat suitability focus on density comparisons, assuming that density decreases from more suitable to less suitable habitat (Andrewartha and Birch, 1954; Wynne-Edwards, 1962; Flather and Hoekstra, 1985). Measures of reproductive success and survival are important indicators of habitat suitability (Van Horne, 1983). Subadult and adult tortoises were recruited into the study population 5-60 yr before the study when habitat conditions may have been different. Inferences from adult and subadult tortoise densities may not always be indicators of areas suitable for reproductive success. Our results suggested some recruitment of tortoises occurred recently across a range of habitat conditions based on hatchling and juvenile burrows.

Other studies used untested correction factors (for review see Burke and Cox, 1988; Burke, 1989) or reported densities within colonies rather than average densities by habitat; thus, densities are not compared easily across studies. Areas of habitat needed to maintain a population size of 40–50 individuals was estimated to be 10–20 ha (Cox et al., 1987) based on home ranges in sandhill (McRae et al., 1981). Tortoises may require at least 30–35 ha of scrub to support 40–50 adults and subadults, based on average densities at KSC. Additional secondary habitat, such as marshes, may be needed because marshes may provide an important food source.

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